Biological Synopsis of the Compound Sea Squirt (*Diplosoma listerianum*)

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2011

Canadian Manuscript Report of Fisheries and Aquatic Sciences 2966

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Cat. No. Fs 97-4/2966E ISSN 0706-6473 (print version)
Cat. No. Fs 97-4/2966E-PDF ISSN 1488-5387 (online version)

Correct citation for this publication:

Mackenzie, A.B. 2011. Biological synopsis of the compound sea squirt (*Diplosoma listerianum*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2966: v + 18 p.

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ABSTRACT

Mackenzie, A.B. 2011. Biological synopsis of the compound sea squirt (*Diplosoma listerianum*). Can. Manuscr. Rep. Fish. Aquat. Sci. 2966: v + 18 p.

Diplosoma listerianum, commonly known as the compound sea squirt, is thought to be native to Europe. The species has achieved a nearly cosmopolitan distribution and was recorded in Atlantic Canadian waters in 2008 off the Magdalen Islands. The main vector for its introduction is through hull fouling. This colonial ascidian has many attributes which make it a successful invader, including its high recruitment rate and ability to migrate after settling. Following its introduction to new habitats, this ascidian rapidly dominates over native species, resulting in species composition shifts and reduced biodiversity. Colonies expand through asexual reproduction, and disperse through sexually produced lecithotrophic larvae. The species can tolerate a wide range of environmental conditions, but thrives in warmer waters. Events such as urban development and fishing create disturbances on the seafloor which facilitate the successful establishment of *D. listerianum*. General control methods have been successful for similar species and need to be studied for potential infestations of *Diplosoma listerianum*. This biological synopsis was prepared as a comprehensive collection of information.

RÉSUMÉ

Mackenzie, A.B. 2011. Biological synopsis of the compound sea squirt *Diplosoma listerianum*. Can. Manuscr. Rep. Fish. Aquat. Sci. 2966: v + 18 p.

Diplosoma listerianum, communément appelée Diplosoma, serait indigène d'Europe. La distribution de cette espèce est maintenant presque cosmopolite et sa présence a été enregistrée en 2008 dans les eaux canadiennes de l'Atlantique au large des Îles de la Madeleine. Le principal vecteur d'introduction vient de sa fixation à la coque des navires. Ce tunicier colonial a plusieurs attributs lui permettant d'être un envahisseur efficace, dont son taux de recrutement élevé et sa capacité à migrer après sa fixation. Suivant son introduction dans de nouveaux habitats, ce tunicier s'impose rapidement face aux espèces indigènes, engendrant une modification dans la composition des espèces et réduisant ainsi la biodiversité. Les colonies se développent par reproduction asexuée et se dispersent par l'entremise de larves lécithotrophes produites de façon sexuée. L'espèce peut tolérer une grande variété de conditions environnementales, mais prolifère davantage dans les eaux plus chaudes. Des événements tels le développement urbain ou la pêche créent des perturbations sur le fond de la mer qui ont comme effet de faciliter le succès d'introduction de *D. listerianum*. Les tuniciers coloniaux sont connus comme étant des pestes encrassant les sites d'aquaculture, et *D. listerianum* fait partie de ce groupe. Cette espèce a le potentiel d'augmenter les coûts liés au traitement des mollusques cultivés et ceux associés aux efforts d'atténuation de ces espèces nuisibles, en plus de réduire les rendements de culture par son étalement sur les espèces cultivées. Des méthodes de contrôles générales se sont avérées efficaces pour d'autres espèces similaires à *Diplosoma listerianum* et devraient être étudiées plus en détails. Cette syntèse de la biologie constitue une source d'informations détaillées visant à faciliter les efforts d'atténuation ainsi que la prise de décisions concernant la gestion de cette espèce.

1 INTRODUCTION

Aquatic invasive species (AIS) pose a great risk to native biodiversity. The compound sea squirt *Diplosoma listerianum* (Milne-Edwards, 1841) is a colonial ascidian with many attributes that make it an ideal candidate for invasion in non-indigenous habitats (Altman and Whitlatch 2007). The attributes that make *D. listerianum* such an opportunistic invader have made it a biofouling pest in New England (Dijkstra et al. 2007), the North Sea (Vance et al. 2009), and other western European sites (Ryland and Bishop 1990). The compound sea squirt was recorded in Atlantic Canadian waters for the first time in 2008 (Nathalie Simard, Maurice Lamontagne Institute, Fisheries and Oceans Canada, Mont-Joli, QC, pers. comm.).

The purpose of this biological synopsis is to summarize the information on the native habitat of the compound sea squirt and the effects of its introduction on competition and population dynamics. A discussion of its life history characteristics and potential impacts of an invasion is presented.

1.1 NAME AND CLASSIFICATION

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Tunicata
Class:	Ascidiacea
Order:	Enterogona
Suborder:	Aplousobranchia
Family:	Didemnidae
Genus:	*Diplosoma*
Species:	*Diplosoma listerianum* (ITIS 1996)

Common Name: Compound sea squirt
Synonyms: It should be noted that this species has been referred to as *D. macdonaldi* in many texts (Millar 1982).

1.2 DESCRIPTION

D. listerianum is a colonial tunicate, meaning that it is composed of many small zooids (0.2 cm long) aggregated around large exhalent openings in a thin (1–2 mm), semitransparent, gelatinous sheet called the test (Telnes 2004; Salem Sound Coastwatch 2011). One exhalent opening or atriopore can serve up to 50 zooids (Mackie and Singla 1987), with colonies typically growing to 20 cm (Salem Sound Coastwatch 2011). It is pigmented with spots of yellow, brown, grey, or white (de Kluijver and Ingalsuo 2004; Telnes 2004; Salem Sound Coastwatch 2011) (Figure 1).

Diplosoma listerianum is a colonial, cryptogenic species (Rocha and Kremer 2005) that may be confused with *Ascidiella aspersa* and *Botryllus schlosseri*. However, *A. aspersa* is a solitary tunicate with a firm bumpy structure, and zooids of *B. schlosseri* align in a star-like pattern to form a light/dark colony (ITIS 1996).

Diplosoma listerianum is a colonial tunicate housing many zooids within a common tunic. The test, or tunic, is formed through secretions of the body wall epithelium, and consists of a matrix of proteins and carbohydrates (including cellulose) (Mackie and Singla 1987). There are blood vessels and sensory processes in the tunic, but no muscles or nerves (Mackie and Singla 1987). The tunic is composed of an upper sheet, which encases the zooids, and a lower (basal) sheet, which is anchored to the substrate by vascular ampullae that form specialized patches of tunic called crampons (Mackie and Singla 1987) (Figure 2). Each zooid is divided into a thorax and abdomen with an oral siphon, a smooth stomach in the abdomen, and an ovary to the left of the gut next to the bilobed testis (de Kluijver and Ingalsuo 2004) (Figure 3). Since the zooids have both sex organs, they are called simultaneous hermaphrodites.

2 DISTRIBUTION

2.1 NATIVE DISTRIBUTION

Diplosoma listerianum is thought to be native to Europe, as it was first described by Milne-Edwards in 1841 from the English Channel (Rocha and Kremer 2005; Salem Sound Coastwatch 2011). Millar (1952) states that it is one of the most common British ascidian species, listing the following coasts as its native habitat: the west and south coasts of Norway, the east coast of the British Isles, the west coast of France, Kattegat, Heligoland, and the Shetland Islands (Millar 1966).

2.2 NON-NATIVE DISTRIBUTION (EXCLUDING CANADA)

The compound sea squirt has achieved a nearly cosmopolitan distribution (de Kluijver and Ingalsuo 2004), and is found on all continents, except Antarctica (Ryland and Bishop 1990) (Figure 4). It has invaded the Brazilian coast (Rocha and Kremer 2005), the south and west coasts of the United Kingdom (Vance et al. 2009), and the Netherlands (Gittenberger 2007). There have also been invasions along the east coast of the United States in the Great Bay estuary (Harris and Dijkstra 2007), and the Gulf of Maine in general (Dijkstra et al. 2007) (Figure 5).

2.3 DISTRIBUTION IN CANADA

The compound sea squirt has been recorded on the west coast of Canada (Kott 2005). In 2008, *D. listerianum* was found in Atlantic Canadian waters for the first time, off the Magdalen Islands (Nathalie Simard, Maurice Lamontagne Institute, Fisheries and Oceans Canada, Mont-Joli, QC, pers. comm.). Locke (2009) included *D. listerianum* on a watch list for potential tunicate invasions to Atlantic Canada. The most likely vector for introduction of this species is hull fouling.

2.4 POTENTIAL VECTORS FOR INTRODUCTION

Many factors influence the success of introduced species. In the past 10–20 years there have been major increases in the number and size of aquaculture facilities, providing more surfaces for colonization (Lambert 2007). There is also a warming trend in waters of temperate regions, which facilitates the growth of invasive ascidians

(Lambert 2007). Shoreline development has also increased, resulting in sediment runoff and providing food directly to suspension feeders, as well as indirectly through eutrophication and phytoplankton blooms (Lambert 2007).

The abundance of colonial ascidians in the Gulf of Maine has increased from 6% to 11% between 1980 and 2005 (Dijkstra et al. 2007). It is thought that *Diplosoma listerianum* invaded the Gulf of Maine in the last 25 years, but was only reported at the Isles of Shoals in 1993 and Portsmouth Harbor in 1999 (Dijkstra et al. 2007).

Since the compound sea squirt has lecithotrophic larvae with short planktonic life stages, it is unlikely to survive in ballast water (Dijkstra et al. 2007). However, juveniles and adults might easily be spread through hull fouling, since there is high recreational vessel traffic in the Isles of Shoals during the summer months (Dijkstra et al. 2007).

3 BIOLOGY AND NATURAL HISTORY

3.1 FEEDING AND RESPIRATION

Diplosoma listerianum is a filter feeder, extracting small particles suspended in the water column through its branchial sacs (Marshall et al. 2003; Lambert 2007). Water is pumped into the inhalant siphon using cilia, and the particles trapped in the mucus net are rolled into a food string and drawn into the oesophagus (Petersen and Svane 2002). The mucus net is produced by the endostyle (Petersen and Svane 2002).

It is estimated that ascidians filter 10–20 litres of water for every millilitre of oxygen consumed, and that each millilitre of oxygen can combust 0.8 mg of food (Barrington 1965). This means that an individual requires 0.05 mg of organic material per litre of seawater filtered to maintain its respiration rate (Barrington 1965). When taking into account other requirements, such as growth and reproductive investment, it is estimated that an individual requires 0.15 mg of food per litre of water (Barrington 1965). This is not an issue for many temperate waters. For example, the English Channel averages 1.6–1.8 mg per litre of particulate matter (Barrington 1965). Ascidians secrete ammonia as a waste (Barrington 1965). Waste is discharged through the anus (Moen and Svensen 2004).

3.2 REPRODUCTION AND DEVELOPMENT

Diplosoma listerianum reproduces both asexually and sexually (Millar 1952). Each colony is established by sexually produced larvae, which metamorphose and produce a colony through asexual budding (Millar 1952; Ryland and Bishop 1990). These two phases tend to alternate with each phase occurring frequently and over a short time span (Berrill 1935).

Asexual budding in the Didemnidae family is known to be more complex than most ascidians. Two centers of budding cells appear midway down the oesophagus; the anterior mass develops a new stomach, intestine, gonads, etc., while the posterior mass develops a new branchial sac (Berrill 1935). The oesophagus separating the two buds then degenerates and the parent body fuses with the new buds, creating two whole and

separate individuals (Berrill 1935). This results in one individual housing the old branchial sac and anterior oesophagus, with the new stomach, intestine, gonads, etc., and the second individual housing the old stomach, intestine, gonads, etc., with the new branchial sac and anterior oesophagus (Berrill 1935). Essentially, the anterior parent body regenerates posterior organs and vice versa, with the epicardium supplying the totipotent cells (Berrill 1935).

The compound sea squirt is also hermaphroditic, meaning individual zooids have both a testis and an ovary (Bishop et al. 1996). The ovary is dorsal and close to the testis, but there is no possibility of direct connection between the sperm duct and ovary in the same zooid. There is evidence, however, of chemotaxis between gametes of other individuals (Burighel and Martinucci 1994a).

The ovary has a branching structure (Bishop and Sommerfeldt 1996). It produces large yolky eggs that are too large to exit via the oviduct (Groepler 2002); therefore, oocytes are brooded within the test and are never exposed to seawater (Bishop and Sommerfeldt 1996). The oocytes mature individually in sequence, so the older eggs are more posterior in the ovary (Burighel and Martinucci 1994a) and are herniated out of the ovarian wall until ovulation (Burighel and Martinucci 1994b).

There has been some controversy over the existence and role of an oviduct in *D. listerianum*. The oviduct runs from the ovary to the atrial space near the anus, flanking the sperm duct (Burighel and Martinucci 1994a; Bishop et al. 1996). Other ascidian species release their eggs through the oviduct, but the compound sea squirt broods its embryos in the tunic (Bishop and Sommerfeldt 1996; Bishop et al. 1996). It is now believed that the main function of the oviduct is to allow sperm to reach oocytes in the ovary (Groepler 2002). There is also a specialized section of the oviduct that is responsible for blocking and destroying sperm from the same zooid (self sperm) (Bishop et al. 1996). Selfing is the most extreme form of inbreeding and can lead to reduced fitness, though it may happen in isolation as an emergency option (Ryland and Bishop 1990). Bishop and Sommerfeldt (1996) reported that this somatic-gametic incompatibility mechanism destroyed self sperm through selected phagocytosis by macrophage cells. The result is a negative correlation between the mating success of pairs and their genetic similarity (Bishop and Sommerfeldt 1996). This mechanism might also be used to reject selected sperm from other external sources (Bishop et al. 1996).

The testis connects to the common ampulla, where the sperm gather before leaving the zooid through a long sperm duct, which terminates at a cloacal opening near the anus (Burighel and Martinucci 1994a). Sperm of this species have a complex structure that is not completely understood (Burighel and Martinucci 1994a). They have a dense spiral groove, which undergoes metamorphosis when it passes through the ovary and is modified over a short period of time by the mitochondrion moving from the head to the tail (Burighel and Martinucci 1994a, b). These changes, called the 'sperm reaction', are triggered by contact with the vitelline coat (Burighel and Martinucci 1994a, b). The

spiral head is thought to improve mobility along the narrow oviduct and penetration of the oocyte (Burighel and Martinucci 1994a).

Diplosoma listerianum has true internal fertilization (Bishop et al. 1996). Sperm travel up the oviduct after about 3 hours of entering the zooid, moving through the blind branches of the ovary for an additional 6.6 hours, and staying next to the oocyte until fertilization occurs (Bishop and Sommerfeldt 1996; Bishop et al. 1996). Sperm from multiple sources may be drawn to zooids by chemotaxis from the oocyte and can be stored within the lumen for up to a month, allowing 7–12 days between ovulations (Bishop and Ryland 1991; Bishop and Sommerfeldt 1996). Storing sperm removes the need for synchronization of gamete maturation (Bishop and Ryland 1991).

Once fertilized, the embryos brood in the colonial test. Ryland and Bishop (1990) observed developing embryos and recorded the presence of segmented tails 7 days after ovulation. Many authors report that this developmental stage is as short as 2 or 3 days, or as long as 1 month before a diurnally controlled release (Brunetti et al. 1988; Burighel and Martinucci 1994a). During periods of high light intensity, larvae make clockspring-like oscillatory movements by contracting their caudal muscles in order to break open the tunic (Brunetti et al. 1988).

The larvae are capable of settling immediately after release, but often swim to other locations in order to propagate the species (Bennett and Marshall 2005). Light plays a role in the length of the pelagic stage, with larvae delaying settlement when kept in the dark, and eventually preferring darker substratum (Brunetti et al. 1988). Marshall et al. (2003) showed that metamorphosis can also be induced by potassium, with 95% of 40 larvae initiating metamorphosis within one hour of exposure.

3.3 LIFE CYCLE: GROWTH, GENERATION TIME, AND LONGEVITY

Many authors have attempted to quantify the life cycle of *Diplosoma listerianum*, with varied results. Millar (1952) concluded that the number of generations per year varies greatly with local and seasonal conditions, namely temperature, so the life cycle of the species will vary with each location.

In the Ardrossan Harbour of Ayrshire, Millar (1952) found one principal and one minor generation. Growth was fastest during the summer months of May, June, and July, with no growth in the winter months (Millar 1952). The complete life cycle from settlement to death ranged 12–18 months (Millar 1952). Settlement of the new generation coincided with the senescence of old colonies, with some zooids remaining in the parent tunic to create composite colonies (Millar 1952).

In the Lagoon of Venice, Brunetti et al. (1988) found three sexual generations, two during the summer and one during the fall. The first two generations had short life spans of 1 to 3 months, while the fall generation survived for 6 to 7 months (Brunetti et al. 1988). The fall generation underwent sexual reproduction in the spring, followed by senescence within the month (Brunetti et al. 1988). More information is needed regarding the breeding season in temperate waters in relation to Atlantic Canada.

Growth of *Diplosoma listerianum* is best measured through expansion of surface area, since colonies rarely grow in thickness, but rather grow out through asexual budding (Brunetti et al. 1988). Millar (1952) reported a maximum surface area 1000–1500 mm^2 during June. Growth rates are maximal during the first month of settlement as a competitive advantage for space (Brunetti et al. 1988). Temperature has a positive influence on blastogenic rate; therefore, high summer temperatures result in extremely high growth rates (Brunetti et al. 1988). This correlation was reinforced by the finding of Agious (2007) that the number of colonies generated is positively correlated with temperature.

The mechanism of sexual reproduction causes an increase in surface area (Brunetti et al. 1988). Zooids increase space between each other in order to make room for brooding larvae in the test (Brunetti et al. 1988).

Compound sea squirt larvae have pooled energy reserves intended for swimming, metamorphosis, and post-metamorphic growth (Bennett and Marshall 2005). Bennett and Marshall (2005) quantified the allocation of these resources, finding 25% of the energy is ear-marked for swimming, and 10% for metamorphosis. Swimming is costly, due to the locomotive structure being a large tail, as opposed to cilia (Bennett and Marshall 2005). Swimming duration was manipulated by Marshall et al. (2003) and Bennett and Marshall (2005) by introducing a shadow to induce vigorous swimming for up to 3 hours. The extended swimming duration robbed energy needed for post-metamorphic growth, resulting in carry-over effects of depleted energy reserves (Marshall et al. 2003; Bennett and Marshall 2005). These carry-over effects included 50% fewer zooids and 10–15% narrower branchial baskets (Marshall et al. 2003).

3.4 HABITAT AND ENVIRONMENTAL TOLERANCES

Diplosoma listerianum grows subtidally from the low water mark to 80 m depth (de Kluijver and Ingalsuo 2004; Salem Sound Coastwatch 2011). It often attaches to algae (*Laminaria* spp. and *Codium fragile*) and eelgrass, as well as any hard substrates, including rocks, vessels, and pontoons (Salem Sound Coastwatch 2011).

Ascidians are usually limited to regions with salinities above 25‰ (Lambert 2007). Osman and Whitlatch (2007) reported that *D. listerianum* disappeared when temperatures fell below -2°C; however, Gittenberger (2007) warns that colonies growing on live animals seem to be more resistant to cold water temperatures than those growing on rocks or plants.

Sexual reproduction is strongly dependent on temperature. Testicle development withstands temperatures 5–7°C, while ovarian development begins at 10°C, with an optimum between 15 and 17°C (Brunetti et al. 1988). Gonad ripening may be delayed at 25°C, which is also the temperature that triggers the death of older generations (Brunetti et al. 1988). Settlement of larvae occurs during high summer temperatures (>15°C) and is halted in the fall with the onset of winter temperatures (Brunetti et al. 1988).

3.5 BEHAVIOUR AND MOVEMENTS

Colonies of the family Didemnidae are capable of locomotion (Mackie and Singla 1987). In unfavourable conditions, the blood vessels retreat up the stalks, which then stretch out and eventually break off (Mackie and Singla 1987). This coincides with the colony swelling when water is trapped in the cloacal space (Mackie and Singla 1987). Stalks in other locations stretch out from <100 µm to 1 mm, allowing their blood vessels with ampullae to form new crampons at new attachment sites in the direction of movement (Mackie and Singla 1987). This behaviour responds to positive phototaxis (Mackie and Singla 1987).

Mackie and Singla (1987) described a network of a new cell type, called myocytes, that are the structural basis for the behavioural action system. This system is sensitive to magnesium, and so it is possible that the cells may communicate through chemical synapses (Mackie and Singla 1987). These cells are found throughout the tunic, but are most concentrated around the cloacal atriopores and the necks of zooids (Mackie and Singla 1987). Zooids take in water and contract their oral siphons independently (Mackie and Singla 1987). When the myocytes are stimulated, there is no response by the individual zooids, but by the colony as a whole (Mackie and Singla 1987). Weak stimulation causes the cloacal atriopores to constrict so that water velocity increases, while strong stimulation can cause the atriopores to close completely (Mackie and Singla 1987). The cells contain actin and conduct impulses very slowly with very long gaps (Mackie and Singla 1987). It is not clear how the regulation of water flow benefits the colony, but it is known that the system has a limited carrying capacity for impulse frequency (Mackie and Singla 1987).

3.6 ECOLOGY

Diplosoma listerianum grows on any hard substrate, including gear and cages on aquaculture sites. Competition for space in benthic communities is high, with the advantage going to fast-growing organisms. The artificial substrates provided by fish farms are prime real estate for settlement and growth for the compound sea squirt, with minimal competition or predation risk (Carman et al. 2010).

There are many potential predators of *Diplosoma listerianum*, including the invasive green crab (*Carcinus maenas*), the Japanese shore crab (*Hemigrapsus sanguineus*), the portly spider crab (*Libinia emarginata*), the Cunner (*Tautogolabrus adspersus*), the lunar dovesnail (*Astyris lunata*), the well-ribbed dovesnail (*Anachis lafresnayi*), and the blood star (*Henricia sanguinolenta*) (Figure 6) (Harris and Tyrrell 2001; Altman and Whitlatch 2007; Dijkstra et al. 2007). With the increase of invasive ascidians comes the potential for increased predatory abundance, which could drive the decline of other prey items from their native habitat (Dijkstra et al. 2007). However, most colonial ascidians are unpalatable to predators, due to their production of chemicals (Dijkstra et al. 2007; Vance et al. 2009). Pisut and Pawlik (2002) studied the taste preferences of the Bluehead Wrasse (*Thalassoma bifasciatum*) for these chemicals deterrents and found that species containing acids deterred the predator from seeking out the tunic, while those with secondary metabolites deterred the predator from selecting the gonads.

Chemical deterrents might also interfere with the growth and settlement of neighbouring organisms (Dijkstra et al. 2007).

3.7 DISEASES AND PARASITES

Little is known about diseases affecting, or caused by, tunicates, but there are records of copepods living parasitically inside ascidians, such as *Haplostoma dudleyae* in the compound ascidian *Eudistoma olivaceum* (Ooishi 1998).

4 HUMAN USES

There are no known uses of *Diplosoma listerianum* specifically, but as it is a primitive chordate, there is value in studying its biology for a better understanding of human biology. Many authors have reported that *D. listerianum* is an excellent experimental organism: the test is almost transparent, allowing live zooids to be directly observed under light microscopy (Bishop and Ryland 1991); the colonies grow rapidly due to asexually budding (Marshall et al. 2003); and the larvae are readily obtained by exposing the colony to light (Marshall et al. 2003).

5 IMPACTS ASSOCIATED WITH INTRODUCTIONS

5.1 IMPACTS ON THE ENVIRONMENT

Coastal and estuarine systems are susceptible to invasions, due to the great variety and abundance of species transported to them, as well as the presence of urbanization stressors such as fisheries, recreational boating, and shipping (Altman and Whitlatch 2007; Harris and Dijkstra 2007). Colonial ascidians have the potential to become dominant over native coastal species within a short period of time (Vance et al. 2009).

Vance et al. (2009) observed the rapid establishment and dominance of *Diplosoma listerianum* when it invaded a new habitat in the North Sea. The first observations recorded patchy distributions for about a month, but, within the following month, percent cover had increased from 6.8% to 59.5%. The fastest growth and highest abundance was seen in July, when the compound sea squirt overgrew many other species; however, *Ascidiella aspersa* and *Umbonula littoralis* were able to resist the overgrowth (Vance et al. 2009).

It is important to understand what factors might facilitate the introduction of non-native species. Altman and Whitlatch (2007) examined disturbance as one of these factors. Disturbances on the seafloor expose spaces, which organisms may exploit for population expansion. Small scale disturbances are often driven by biological processes, such as predation, while large scale disturbances are often driven by physical processes, such as storms or human activities (Altman and Whitlatch 2007). Coastal systems are prone to both types of disturbances, making them particularly susceptible to invasion (Altman and Whitlatch 2007).

Altman and Whitlatch (2007) experimented with different magnitudes and frequencies of disturbances on hard substrates of subtidal communities and observed the behaviours of native and non-native species. They found both increased magnitude and frequency of disturbance had a positive effect on the growth of recent invaders, and a negative effect on resident species, leading to a significant decrease in species richness within one year. *D. listerianum* was the dominant invader, and the success of this species included its ability to fuse with other colonies, to migrate after settling, its high recruitment rate, and its high growth rates in warm water. Altman and Whitlatch (2007) also speculated there may be a competitive advantage to being a new invader, and the dominant response may slow with time.

Another example of how invasive species can affect their environment has been observed in the Gulf of Maine. Harris and Tyrrell (2001) have documented shifts in species composition of the benthic community for 20 years. Large scale disturbances resulting from bottom trawl fishing have facilitated the establishment of many invasive species, and the early succession invaders have contributed to the success of more recent invaders, such as *D. listerianum* (Harris and Tyrrell 2001). The compound sea squirt is now one of the most conspicuous species inhabiting all hard substrates, as well being an epibiont on many algal species (Harris and Tyrrell 2001). Invasive species have replaced native species, resulting in a benthic community that is 33% different in 2006 as compared with 1982 (Harris and Tyrrell 2001).

5.2 IMPACTS ON OTHER SPECIES

There are many effects of introductions on native species, including reduced local biodiversity and the threat of declining abundance of commercially important species (Altman and Whitlatch 2007). It is well known that stable communities with high species richness are far better at resisting invasions (Altman and Whitlatch 2007). There are also indirect effects of non-native establishments, such as shifts in population dynamics and competitive challenges.

As noted above, invasive ascidians have changed the composition of benthic communities in the Gulf of Maine from native to invasive dominated (Dijkstra et al. 2007). The annual peak in abundance occurs during the summer and fall, causing problems for the native species that reproduce, settle, and historically experience high growth rates during this time (Dijkstra et al. 2007). These species now need to compete for space, possibly leading species composition toward homogeneity (Dijkstra et al. 2007).

More direct effects are known to occur, such as the blocking of light and nutrient absorption when *D. listerianum* grows on algae (Harris and Tyrrell 2001).

5.3 IMPACT SUMMARY

Potential impacts due to the establishment of *D. listerianum* invasions are widespread. Coastal ecosystems in particular are vulnerable, and coastal communities need to be vigilant with respect to early detection and mitigation plans. These systems are susceptible to invasions for a variety of reasons, such as high shipping and recreational

traffic, and disturbance events. The compound sea squirt becomes dominant over native species within a short period of time, reducing coastal marine biodiversity and threatening commercially important species. With the increase in populations of invasive ascidians comes the potential for increased predator abundance and many environmental and biological consequences. More information on its life history and environmental tolerances in marine environments similar to those in Atlantic Canada, and timely control methods, will improve the ability to control its potential impacts.

6 CONSERVATION STATUS

Diplosoma listerianum is not listed under the International Union for Conservation of Nature (IUCN) list of threatened species and is therefore considered to be without conservation status (IUCN 2011).

7 SUMMARY

Diplosoma listerianum is an opportunistic species with high growth rates, which allow it to rapidly dominate new habitats. The compound sea squirt can tolerate a wide range of environmental conditions, which is reflected in its nearly cosmopolitan distribution. The recent introduction of *D. listerianum* raises legitimate concerns about threats to native species; however, with early detection and appropriate control measures, the impacts can be controlled.

8 ACKNOWLEDGEMENTS

Thank you to Dawn Sephton (Bedford Institute of Oceanography, Fisheries and Oceans Canada, Dartmouth, Nova Scotia) and Heather Niblock (Centre of Expertise for Aquatic Risk Assessment (CEARA), Fisheries and Oceans Canada, Burlington, Ontario) for their guidance. This synopsis was funded by CEARA, Fisheries and Oceans Canada, Burlington, Ontario.

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(© Bernard Picton 2010)

Figure 1. *Diplosoma listerianum*
(Picton and Morrow 2010)

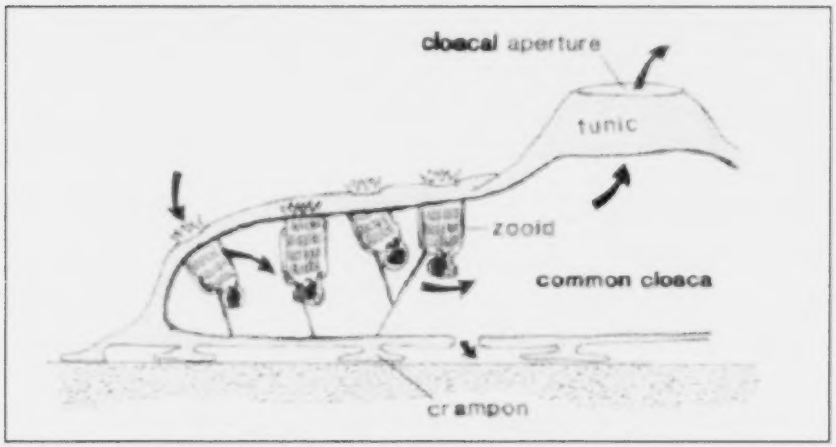

Figure 2. Lateral view of *Diplosoma listerianum*
(caption modified from Mackie and Singla 1987)
(Reproduced with permission from the Marine Biological Laboratory, Woods Hole, MA)

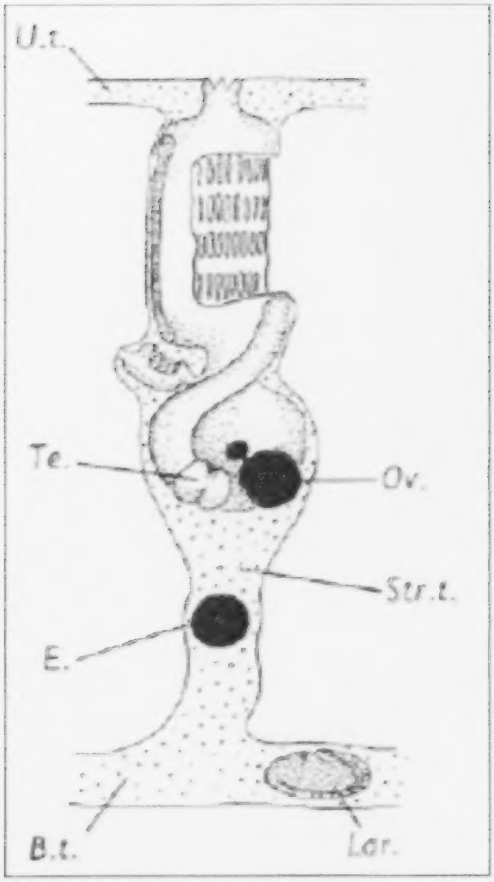

Figure 3. *Diplosoma listerianum* zooid.
B.t. - basal layer of common test; E. - egg; Lar. - larva; Ov. - ovary; Str.t. - strand of common test into stalk; Te. - testis; U.t. - upper layer of common test (Millar 1952)
(Reproduced with permission from Cambridge University Press)

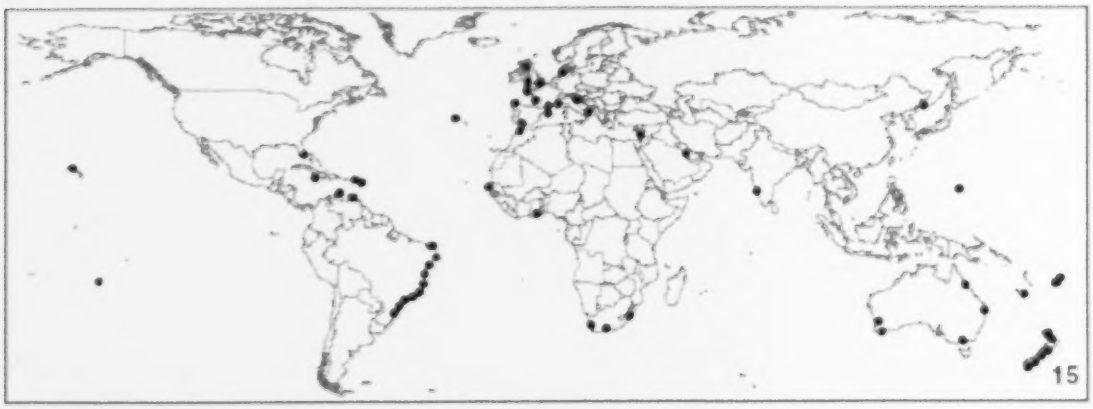

Figure 4. Worldwide distribution of *Diplosoma listerianum*
(Rocha and Kremer 2005)
(permission: http://creativecommons.org/licenses/by-nc/3.0/ accessed October, 2011)

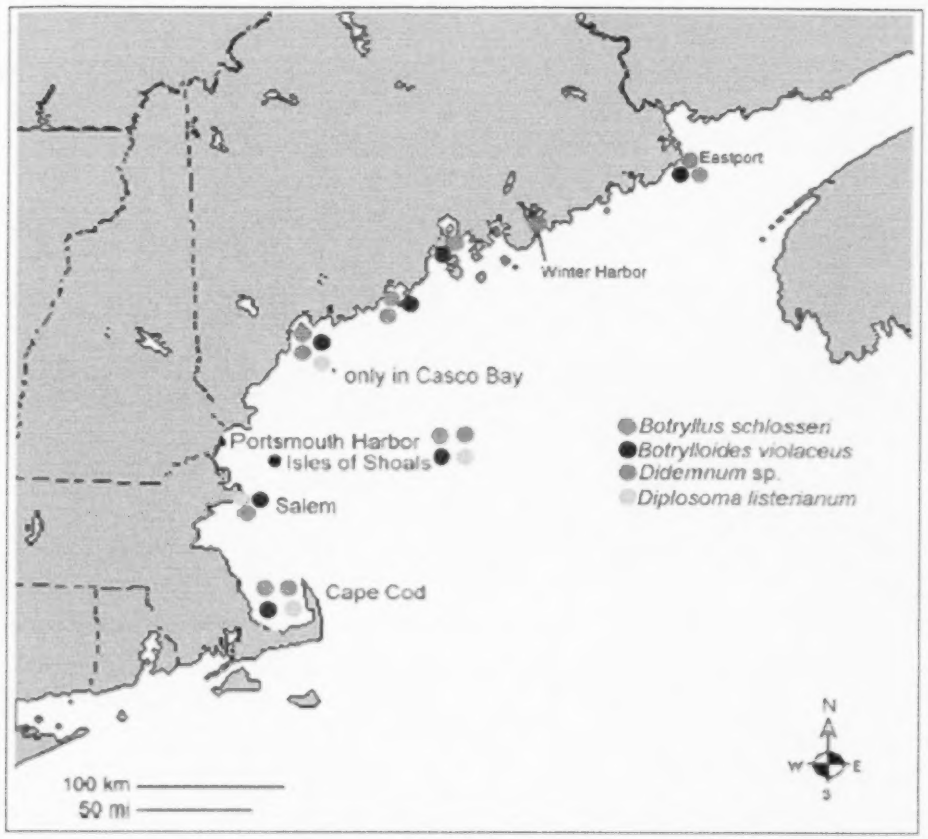

Figure 5. Distribution of *Botryllus schlosseri*, *Botrylloides violaceus*, *Didemnum* sp., and *Diplosoma listerianum* in the Gulf of Maine
(Dijkstra et al. 2007)
(Reproduced with permission of Elsevier Ltd.)

(Photo credit: Larry. G. Harris)

Figure 6. The blood star *Henricia sanguinolenta* feeding on *Diplosoma listerianum* in Portsmouth Harbour

(Harris and Dijkstra 2007)

(Reproduced with permission from the Piscataqua Region Estuaries Partnership)